Revue suisse de Zoologie 108 (4): 919-948; décembre 2001

Hemerophis, a new genus for *Zamenis socotrae* Günther, and a contribution to the phylogeny of Old World racers, whip snakes, and related genera (Reptilia: Squamata: Colubrinae)

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***Hemerophis*, a new genus for *Zamenis socotrae* Günther, and a contribution to the phylogeny of Old World racers, whip snakes and related genera. -** External morphology, skull bones, vertebrae, visceral topography and hemipenis features of the Sokotra racer were examined. Considerable differences exist vis-à-vis Palaearctic and East African racers and the insular species is thus referred to a monotypic genus, *Hemerophis*. The isolated position of *H. socotrae* (Günther, 1881) is confirmed by nucleotide sequences of two mitochondrial genes, cytochrome c oxydase I and 12S rRNA. As to its phylogenetic relationship, *H. socotrae* requires further comparison with Afrotropical colubrids.

Based on morphology and molecular data (mtDNA), the whip snake *Tyria najadum* Eichwald and related eastern Mediterranean species, the East African *Coluber florulentus* group, and the Arabian endemics *Zamenis elegantissimus* Günther and *Z. variabilis* Boulenger are referred to *Platyceps* Blyth. *Hemorrhois* Boie is composed of the western *H. algirus* (Jan) and *H. hippocrepis* (Linnaeus), and an eastern subgroup with *H. nummifer* (Reuss) and *H. ravergieri* (Ménétries). *Hemorrhois* and *Platyceps* spp. belong to a monophyletic group including the mainly Saharo-Sindian genus *Spalerosophis* Jan.

The composition and systematic content of *Hierophis* Fitzinger remain unclear. To judge from mtDNA data, eastern Mediterranean species including *H. caspius* (Gmelin) are much closer to *Eirenis modestus* (Martin) than to the purely European *H. gemonensis* (Laurenti) and *H. viridiflavus* (Lacépède). Additional studies with more taxa are necessary to scrutinize the sister group relationship of *Eirenis* Jan with *Hierophis* spp. and to assess their phylogenetic affinities with other Palaearctic racer genera.

Key-words: *Hemerophis* gen. n. – *Eirenis* – *Hemorrhois* – *Hierophis* – *Platyceps* – *Spalerosophis* – morphology – mtDNA – phylogeny – Sokotra.

Manuscript accepted 09.07.2001

INTRODUCTION

The colubrine *Zamenis socotrae* Günther, 1881 is endemic to the Sokotra archipelago off the Horn of Africa. Günther (1881) thought that this species "is most nearly allied to" the western Arabian *Z. elegantissimus* Günther.

Parker (1949) noted that "the very striking similarity in colour pattern undoubtedly played a part, perhaps an unduly large part, in influencing Dr. Günther to this conclusion". He had "little doubt" that *Coluber* (sensu lato) *socotrae* "is allied to the *florulentus* group of species (including *elegantissimus*) which it resembles in its lepidosis and colour pattern" (Parker, 1949). This opinion has been followed by Schätti & Desvoignes (1999) who pleaded for affinities of the species from Sokotra with East African racers of the *C.* (s. l.) *florulentus* group. Based on cytochrome b sequences, Nagy *et al.* (2000) concluded a different origin of *C.* (s. l.) *socotrae* and Palaearctic racers.

Many Palaearctic species formerly grouped in *Coluber* (sensu Schätti & Wilson, 1986) belong to the genera *Hemorrhois* Boie, *Hierophis* Fitzinger and *Platyceps* Blyth (Schätti, 1986a, 1987, 1988a, 1988b, 1993a). For reasons explained elsewhere (Schätti & McCarthy, 2001; Schätti *et al.*, 2001), the whip snake *Tyria najadum* Eichwald and related species have so far been assigned to *Coluber* sensu lato. This nomen operandum has also been applied to a few racers with hitherto unclarified affinities including Arabian endemics (e.g., *Zamenis elegantissimus* Günther) and the mainly Afrotropical *florulentus* group (Schätti, 2001b) as well as endemic species of the western Sahel, the Horn of Africa, and Namibia (Broadley & Schätti, 1999).

This paper gives a detailed description of *Coluber* (s. l.) *socotrae* and a morphological comparison with Old World racers. The main purpose is to assess the systematic status of the insular taxon and its relationship with Palaearctic and East African racer genera. Their phylogenetic affinities are evaluated on the basis of molecular data from twenty species of the genera *Hemorrhois*, *Hierophis*, and *Platyceps*, the Sokotra racer as well as one representative each of the assumedly related Palaearctic genera *Eirenis* Jan and *Spalerosophis* Jan.

MATERIAL AND METHODS

External morphological features were studied in a total of 27 specimens of *Coluber* (s. l.) *socotrae* including two living individuals. The preserved material is deposited in the following institutions: The Natural History Museum, London (BMNH), Museum of Comparative Zoology, Cambridge (MCZ), Muséum d'Histoire naturelle, Geneva (MHNG), Museo zoologico dell'Università (La Specola), Florence (MZUF), Naturhistorisches Museum, Vienna (NMW), and Zoologisches Museum der Universität Hamburg (ZMH).

The examined specimens (n=28) are: BMNH 1946.1.14.97-99: "Socotra" (type series, l. B. Balfour 1880); BMNH 99.12.5.119: "Hadibu Plain" [Hawlaf] (halfgrown ♀, W. R. Ogilvie-Grant & H. O. Forbes 1898/99); BMNH 1953.1.8.24: "Socotra" (hgr. ♀, G. B. Popov March 1953); BMNH 1962.936-937: "Socotra" (♂, juv., N. L. Corkill) [1962.936: skull, vertebra, ventral 75]; BMNH 1965.1460: "Wadi Ashur, Dihams Plain, W. Socotra" (hgr. ♀, "Joint Services Exp. Socotra 1964", i.e., Royal

Geographic Society & Royal Air Force expedition). MCZ 25884: "Socotra" (♀, O. Simony 1898/99). MHNG 2443.4: Hadibu ["Tamarida", see text] (♂, E. Riebeck & G. Schweinfurth 1881, formerly ZMH 2506); MHNG 2581.92: lower Wadi Di-Farhoh (♂, B. Schätti March 1995) [midbody vertebrae]; MHNG 2610.88: Wadi Qishn, c. 250 m (♂, B. Schätti April 2000) [skull]; MHNG 2610.89-90: Fikhah [Ras Momi] (♂♀, B. Schätti April 2000, living specimens). MZUF 4470: "Hanefu R.[iver]" [Wadi Manifoh] (♂, G. B. Popov 1953, formerly BMNH 1953.1.8.25). NMW 25447.1-5: Samhah ("Insel Samheb", ♂, ♀♀, O. Simony January 1899); NMW 25447.6-8: Ras Shuab (♂♂, ♀, O. Simony January 1899) [25447.8: skull]; NMW 25447.9-10: Hawlaf (♂♂, O. Simony February 1899); NMW 25449: Aqarhi ["Hakari nächst der Mündung des Wadi Felink", Steindachner, 1903] (♂, O. Simony 1899) [vertebra, ventral 140]; NMW 25467: Qalansiyah (♂, O. Simony January 1899). ZMH 2507: Hadibu ["Tamarida", see text] (♂, E. Riebeck & G. Schweinfurth).

Methods and definitions used in the descriptive part are explained in Schätti (1987, 1988b). The term subtemporal denotes the scale situated between the posterior supralabial and anterior temporal scales; anteriorly, it borders the lower postocular and the posterior subocular. The subtemporal corresponds to the upper part of the supralabial that follows the posterior subocular, i.e., usually the seventh. Its posterior tip may or may not touch the lowest temporal of the second row. Except for its usually smaller size, the subtemporal cannot be properly distinguished from the anterior temporals.

Vertebra measurements and their abbreviations used in the text are: length of centrum (lc), length of neural crest (nc), least width of neural arch (wn), and width across prezygapophyses between outer edge of articular facets (wp). These measurements as well as further vertebra features used in the following text are explained and figured in Auffenberg (1963) and Helfenberger (2001). Anatomical data and the position of dorsal scale row reductions along the body (i.e., mean counts of right and left side values) are given in terms of ventrals and in percent of their total number (% vs). The length of the hemipenis and the *M. retractor penis magnus* are expressed in absolute numbers of subcaudals and as a percentage thereof (% cs). We follow Dowling & Savage (1960) with regard to hemipenis terminology.

Osteological data and descriptions are based on a limited number of specimens (see text). Apart from a few circumstantial observations, visceral features of *Hemerophis socotrae* were examined in five males and a single female specimen, i.e., MHNG 2610.88, NMW 25447.2 (♀), NMW 25447.5, and NMW 25447.8-10.

A more detailed synonymy of the Sokotra racer and coordinates of the collecting sites are given in Schätti & Desvoignes (1999). The pertinent references for morphological characters of Palaearctic and Afrotropical racers discussed in this study are quoted at their appropriate place in the following text.

The "*Coluber florulentus* group" is made up of the name bearing species and a number of mainly East African taxa (e.g., *Zamenis b. brevis* Boulenger, *Z. b. smithi* Boulenger [see Schätti in Lanza, 1990], *C. taylori* Parker) including *C.* (s. l.) *largeni* Schätti from the Dahlak archipelago (Schätti, 1988b, 2001b). *C.* (s. l.) *florulentus*

perreti (Schätti) from Cameroon and Nigeria might be a valid species. For the purpose of this paper, the Saharo-Sindian region is considered to be part of the Palaearctic realm.

Besides *Hemerophis socotrae*, the mitochondrial genes cytochrome c oxydase I (COI) and 12S rRNA of seventeen Palaearctic and Afrotropical racers as well as *Eirenis modestus*, *Spalerosophis diadema*, and *Coelognathus* [*Elaphe*] *flavolineatus* (see Helfenberger, 2001) were sequenced (see Appendix). All except an endemic Arabian taxon (*variabilis*) were included in the phylogenetic analyses (Figs 8-9). Among various colubrid taxa evaluated (e.g., *Elaphe* spp. sensu Helfenberger, *Ptyas korros*), the Indo-Malayan *C. flavolineatus* (Schlegel) turned out to be most appropriate as an outgroup for the present study. Its basal position vis-à-vis the examined racer taxa was checked including the phylogenetically more distant *Dinodon semicarinatus* (Cope). The scientific names of the taxa with their author and year of description are listed in the Appendix compiling the tissue samples used for the present study.

MtDNA was isolated from fresh liver tissue (Spolsky & Uzzell, 1986) and purified by phenol/chloroform extraction and ethanol precipitation (Maniatis *et al.*, 1982). Pure mtDNA was re-suspended in TE buffer (10mM Tris-HCl, pH 8, 1mM Na_2EDTA) and stored at -70°C. For some specimens (see Appendix) genomic DNA was extracted from shed skin, liver preserved in 70% ethanol, or frozen muscle using the DNeasy Tissue Kit from Qiagen. Highest DNA yields from shed skin were obtained with Protocol A for isolation of genomic DNA from insects (Qiagen).

Two fragments of the mitochondrial genome, viz. 12S rDNA and COI, were amplified using the polymerase chain reaction (PCR) under the following conditions: a total volume of 50µl contained 1 x PCR buffer, 200µM of each dNTP (Roche), 0.6µM of each primer, 2.5 u *Taq* polymerase (Qiagen), and either 1 x Q-Solution (Qiagen, for 12S rDNA) or 2mM $MgCl_2$ (COI). PCR primers applied are 12S268(+), 5'-GTGCCAGCGACCGCGGTTACACG-3', 12S916(-), 5'-GTACGCTTACCAT GTTACGACTTGCCCTG-3', COI(+)deg1, 5'-AAGCTTCTGACTNCTACCACC NGC-3', and COI(-)bdeg, 5'-ATTATTGTTGCYGCTGTRAARTAGGCTCG-3'.

All primers were developed by the junior author (Utiger, in prep.). PCR was performed with a PTC-100™ thermocycler (MJ Research, Inc.) using the following thermal profile: 3 min at 94°C, followed by 35 cycles of 1 min at 94°C, 1 min at 65°C, 1 min at 72°C, and a final step of 10 min at 72°C. Double-stranded PCR products were purified with the QIAquick PCR Purification Kit (Qiagen) and both strands were sequenced following the ABI Prism® BigDye™ Terminator Cycle Sequencing Ready Reaction Kit protocol, version 2.0, using the ABI 377 automated sequencing system (PE Biosystems). The 12S rDNA has 677 base pairs including primers, COI 632. The fragments correspond to the positions 303-980 and 6519-7151, respectively, of *Dinodon semicarinatus* (GENBANK accession No. NC 001945). The DNA sequences of all individuals except MHNG 2456.71 (*variabilis*) are deposited in the GENBANK (accession numbers AYO39126-39201). The alignment data file is available from the junior author's homepage (www.unizh.ch/ zoolmus/eHerpetologie.html).

A total of 610 positions including insertions or deletions (indels) of the 12S rDNA and 513 base pairs of COI sequences of 38 individuals belonging to twenty

species were edited with the *Seqlab* program of the Wisconsin Package (Genetics Computer Group, 1999) and aligned with Clustal X (Thompson *et al.*, 1994). The initial alignment of the 12S rDNA fragment was improved in a second step using the aligned sequences of *Alligator mississippiensis* and *Homo sapiens* (Maidak *et al.*, 2000) as well as the secondary structure information of *H. sapiens* (Gutell *et al.*, in prep.) and the scincid lizard *Oligosoma nigriplantare polychroma* (Hickson *et al.*, 1996). The alignment includes 29 indels at 19 different regions and is unambiguous. Thirteen of them consist of one position, two of two positions, and four indels of three.

Phylogenetic analyses and descriptive statistics were performed with PAUP* versions 4.0b4a, 4.0b5, and 4.0b6 (Swofford, 1998). The pattern of DNA evolution between two taxa and the probability of saturation effects were examined separately for each codon position of the amplified COI gene fragment, as well as for the entire sequence in both the COI and 12S rRNA genes.

For the 12S rDNA fragment, 224 (207 without indels) of 610 (581) aligned sites are variable and 171 (162) parsimony informative including gaps as a fifth character state. The ranges of base frequencies of the L-strand are 39.3-41.3% (mean: 40.4%) for A, 22.0-25.6% (23.9%) C, 18.3-20.5% (19.5%) G, and 15.5-17.3% (16.2%) T. The values for the coding L-strand of the COI fragment (513 aligned sites) are 186, 179, and 25.9-29.8% (28.4%) A, 24.4-29.2% (26.9%) C, 14.6-17.2% (15.9%) G, and 27.2-31.4% (28.7%) T, respectively. Uncorrected pairwise sequence divergence of COI was plotted against the same measure of 12S rDNA (Fig. 1). In contrast to the substitution values for 12S rDNA, which increase without an apparent upper limit, COI shows considerable saturation tendency by losing the linear correlation with 12S rDNA at approximately 14% and tapering off to a value of 17% (Fig. 1). The third position of the codon is responsible for most of the overall variation (87.6%). Whereas there is no substitution in the second position at all, relatively few first position changes are observed (12.4%).

The model of DNA evolution which best fits the data under the maximum likelihood criterion was estimated with the program MODELTEST (Posada & Crandall, 1998). For phylogenetic reconstruction, maximum likelihood, maximum parsimony and neighbour joining methods were performed with PAUP*. Neighbour joining and maximum likelihood analyses were executed with heuristic searches, tree-bisection reconnection (TBR) branch swapping, and different models of evolution. The latter include the general time-reversible (GTR), the Hasegawa-Kishino-Yano (HKY), and the Jukes-Cantor model (Hasegawa *et al.*, 1985; Jukes & Cantor, 1969; Kishino & Hasegawa, 1989). The GTR+G+I model assumes that substitution rates follow a γ distribution with shape parameter α (G), and that some sites are invariable with proportion (I), estimated via maximum likelihood. Nonparametric bootstrap values (Felsenstein, 1985) were calculated including 1000 replicates for neighbour joining and maximum parsimony, and 100 replicates using the faststep search option for the maximum likelihood method. Heuristic maximum parsimony analysis with TBR branch swapping was performed treating gaps as a fifth character state.

In order to determine whether the phylogenetic information contained in the two data sets (partitions) was significantly different, the incongruence length

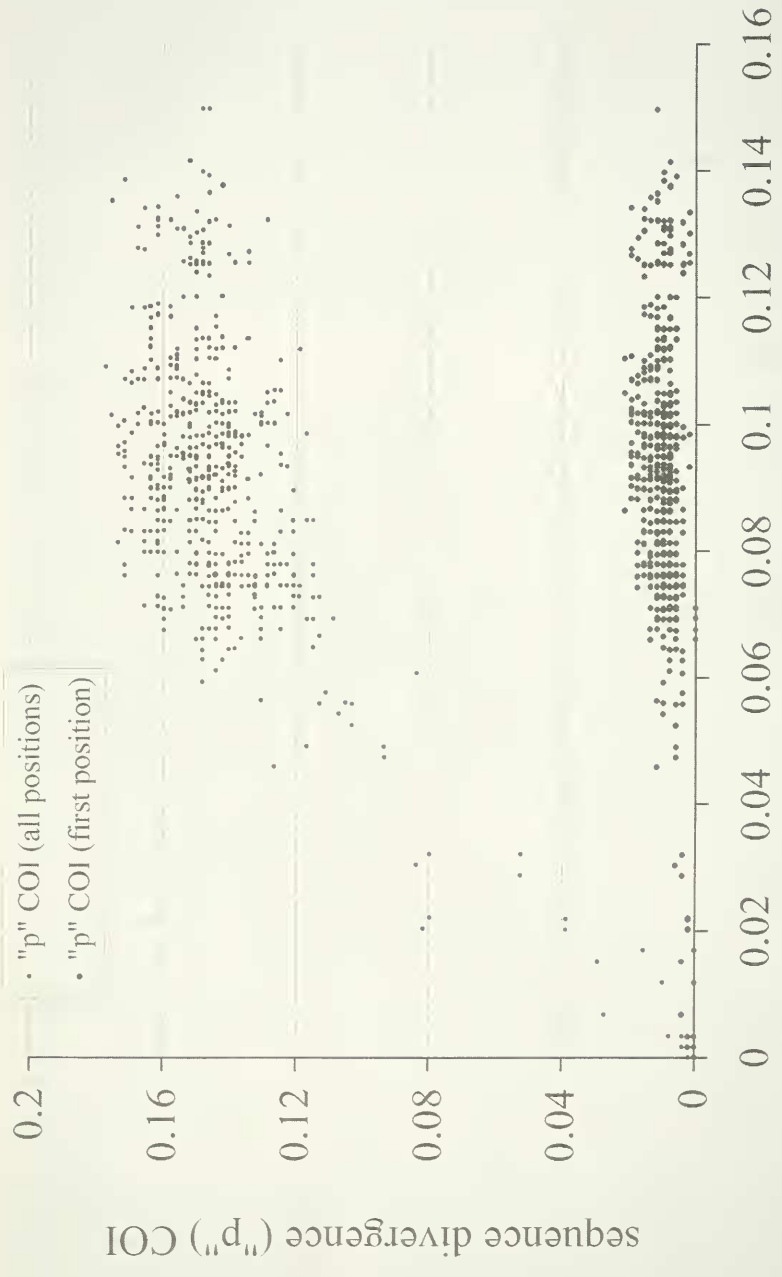


FIG. 1. Uncorrected pairwise sequence divergences "p" of the coding COI versus "p" of 12S rDNA.

difference test (ILD test, Farris *et al.*, 1995), implemented as partition homogeneity test in PAUP*, was performed with ten random stepwise additions using TBR branch swapping and 1000 randomisations. If the data sets were not significantly different, it was assumed that both data sets provide an estimate of the same phylogenetic tree and, therefore, can be combined for subsequent analyses. Significantly incongruent data sets should be analysed separately (e.g., Vidal & Lecointre, 1998).

However, it is often unclear whether a significant test value stems from real incongruence due to a structured contradictory signal or results from random noise that arises from multiple substitutions at particular sites. The latter can produce highly significant results in the ILD test as demonstrated by Dolphin *et al.* (2000). To differentiate between these two phenomenons, these authors described a procedure using randomly generated data sets.

The operation of Dolphin *et al.* (2000) was slightly adapted for our analysis. For all investigated taxa, the character states of ten, twenty, thirty, forty and fifty randomly chosen, variable, parsimony informative characters of one gene were shuffled successively in Microsoft Excel to produce partially randomized data sets. Eight runs of this procedure were performed, and the ILD test was executed with the original data set of one partition and a shuffled data set of the other one. The *P* value resulting from this procedure was plotted against the number of shuffled characters and regressions were calculated. To determine the behaviour of the *P* values with increasing number of shuffled characters, it was tested whether the slope of the regression line is different from zero.

If randomizing the noisier data set increases the significance of conflict, an assessment of real incongruence is difficult to make (K. Dolphin, pers. comm.). On the other hand, increasing *P* values from the ILD test, with the less noisy data set shuffled, indicate that both the permutated and the already noisy data set contain the same random information as found in the partitions for the null length distribution of the ILD test.

RESULTS

The species from Sokotra differs in many respects from Palaearctic and Afrotropical racers and whip snakes and is herewith referred to a new monotypic genus.

Hemerophis gen. n.

Derivatio nominis. This genus is named for its placid nature. *Hemerophis* stems from the Greek words *hemeros* (ημερος), meaning mild, gentle, or kind, and *ophis* (οφις), i.e., snake; the gender is masculine.

Diagnosis. Nine to eleven supralabials, one (usually fifth) in contact with eye. Preocular normally paired; with a posterior subocular (much larger than anterior subocular) and a subtemporal scale; posterior chin shields often reduced. Dorsals smooth, with paired apical pits; second longitudinal row made up of comparatively large and interspersed smaller scales; 23 longitudinal rows on neck (25th ventral),

23 at midbody and 17 (rarely 15) prior to anal plate; posterior reductions involving lower lateral (one pair) and paravertebral (two pairs) levels. 217-237 ventral scales, 112-125 subcaudals (sexual dimorphism insignificant). 17-20 maxillary teeth, diastema varies in size, last tooth not or only slightly offset laterad; pterygoid with 23-28 teeth. Median processus of palatinum not reaching beyond anterior border of choanal processus. Parasphenoid basally constricted, postero-lateral area of basisphenoid distinctly emarginated. Least width of neural arch of midbody vertebrae 1.3 to 1.4 times in centrum length. Posterior organs, particularly gonads (i.e., testes) and kidneys, shifted backwards vis-à-vis Palaearctic and Afrotropical racers. Hemipenis comparatively short, subcylindrical, basally spinose, with distinct apical depressions; sulcus spermaticus simple. A single species from Sokotra and Samhah Island is known.

Hemerophis socotrae (Günther, 1881)

Zamenis socotrae Günther, 1881: 463, Plate 41. – "Socotra" (three syntypes).
Zamenis socotrae. – Peters, 1882: 46 ("Socotra"); Boulenger, 1893: 408 ("types").
Zamenis sokotrae [sic]. – Steindachner, 1903: 14 (Aqarhi, Hawlaf, Qalansiyah, Ras Shuab, Samhah).
Zamenis socotrae. – Werner, 1929: 65, 70 ("Sokotra").
Coluber socotrae. – Parker, 1949: 44 (review, relationship); Corkill & Cochrane, 1966: 484 (Hadibu, "Hanefu" [Wadi Manifoh], "Hasu").
Coluber socotranus [sic]. – Balletto, 1968: 212 (biogeography).
Haemorrhois [sic] *socotrae*. – Welch, 1982: 155 (checklist).
Eremiophis socotrae. – Welch, 1983: 108 (Old World racer genera [nomen dubium]).
Coluber socotrae. – Schätti & Wilson, 1986: 399 (checklist, key).
Coluber (sensu lato) *socotrae*. – Schätti & Desvoignes, 1999: [101] 125 (Sokotra reptiles).

Description. Rostral broader than deep. Internasals smaller and shorter than prefrontals. Frontal longer than its distance from the tip of the snout, at least one and a half times as long as wide, broad in front, usually not in contact with the upper preocular, lateral margins slightly concave (i.e., bell-shaped). Parietals longer than frontal, truncated behind.

Nasal divided, upper border of nostril in contact with internasal. Loreal pentagonal (sometimes hexagonal), distinctly longer than wide, posterior part situated below upper preocular. Usually ten (nine to eleven) supralabials, fifth or sixth entering orbit (Fig. 2). Normally two preoculars, upper larger; suture in some cases incomplete or, rarely, with only a single preocular (MHNG 2610.89). Anterior subocular more or less the same size as lower preocular. MZUF 4470 with an additional small scale between the anterior subocular and loreal on the left side. Two postoculars, lower somewhat smaller. Posterior subocular larger than postoculars, usually corresponding to upper part of sixth supralabial; NMW 25447.10 with two posterior suboculars of smaller than usual size (Fig. 2B).

Arrangement and size of scales in the temporal region variable (Fig. 2). Subtemporal usually situated above seventh supralabial, mostly in contact with lower postocular (see Material and methods). Usually two enlarged temporals in first row, and sometimes up to four including subtemporal; a single proper anterior temporal, wider than long, on left side of BMNH 1946.1.14.99 (syntype). Second row of temporals made up of three or four scales.

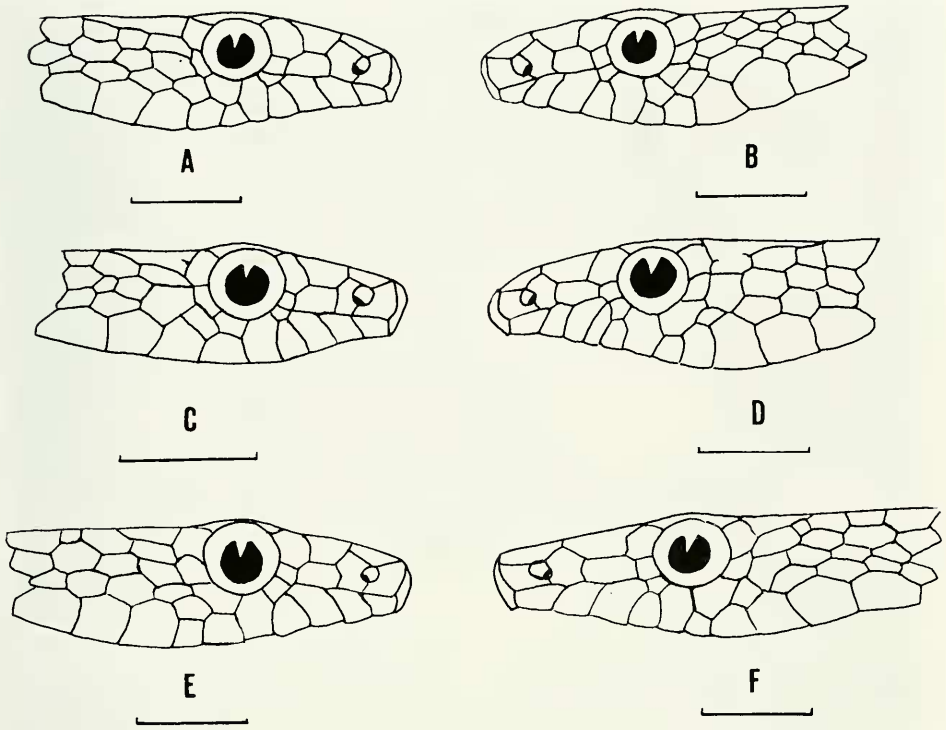


FIG. 2

Lateral view of upper head scales in *Hemerophis socotrae*. NMW 25447.1 (A), NMW 25447.10 (B), NMW 25447.3 (C), NMW 25467 (D), NMW 25447.9 (E), and NMW 25449 (F). Scale (line): 5 mm.

Ten to twelve sublabials, four or five anteriormost on each side in contact with first pair of chin shields, sixth or seventh (rarely fifth or eighth) largest. Posterior chin-shields narrow and usually separated from each other by two to five sometimes concealed series of scales of different size and shape; more or less equal in length to anterior chin shields but in some cases distinctly reduced in size (e.g., MHNG 2610.90), divided (NMW 25447.8) or virtually absent (MCZ 25884). Normally with five to six (rarely four) rows of scales running obliquely between the posterior end of the chin shields and the first ventral scale.

Dorsal scales smooth (not keeled as inadvertently stated in Schätti & Desvoignes (1999) and mixed up with *Ditypophis vivax* in their key and text) and with two apical pits. First longitudinal row composed of enlarged scales. Second row made up of comparatively large scales vis-à-vis those on flanks and back and irregularly interspersed scales of significantly smaller size. Normally in 25 rows across body at level of tenth ventral, 23 rows at 25th ventral and midbody and 17 rows five ventrals prior to cloaca. Reduction on neck involves second and third or third and fourth row between ventral 15 and 23 (7-10% vs) in males, and 14-22 (6-8%) in females, respectively (see Material and methods). Exceptions from this pattern are

found in four males: NMW 25447.8 discards third row already at the ninth ventral; paravertebral rows, between ventrals 12-17, are involved in NMW 25447.10; MHNG 2581.92 and NMW 25467 (ventrals 85-100) have partly 24 dorsals near midbody due to anomalies in the vertebral row.

First and second reduction of dorsal scales on posterior part of body involving lower lateral (usually second and third row, exceptionally first and second in BMNH 1953.1.8.24) and paravertebral rows of variable sequence between ventral 120 and 156 (53-68% vs) in males, and 124-141 (53-62%) in females. Reduction from 19 to 17 longitudinal rows invariably paravertebral, situated between ventral 175 and 202 (means of right and left side, extremes 167-214) or 77-88% in males, and 170-191.5 (extremes 159-203) or 75-83% in females. NMW 25447.6 (♂, 22 rows at ventral 120) with a fourth posterior reduction to 15 dorsal scales including second and third row at ventral 213 (94% vs).

Ventrals 217-237 (♂♂ 222-231, ♀♀ 217-237); anal plate divided; 112-125 (118-125, 112-123) usually paired subcaudals (anterior ones partly single in NMW 25447.4). Corkill & Cochrane (1966) noted 133 subcaudals in an individual collected by N. L. Corkill. However, the specimens obtained by this collector (BMNH 1962.936-937) have 118 (juvenile) and 122 (♂) subcaudals, respectively.

Maximum total length in males 1480 mm (1110 + 370 mm, MZUF 4470), females 1007 mm (760 + 247 mm, NMW 25447.4). Tail / body length ratio (including head) in preserved specimens 0.33-0.38 (♂♂) and 0.32-0.37 (♀♀); 0.34 in a subadult (340 + 115 mm, MCZ 25884).

Pileus olive, dark brown or black. Snout sometimes greyish brown or olive above, with two narrow transverse lighter bars along the posterior border of the internasals (may be conspicuously white, see Plate 1) and between the preoculars. Freno-parietal, temporal and nuchal region often uniformly darkened. Loreal area may be olive or light brown. Supralabials, preocular and postocular predominantly whitish, or periocular region with a hazel tinge. Supralabials sometimes with very fine black lines along their adjoining edges. Chin and throat whitish, light yellow or, posteriorly, with an orange hue.

Dorsal colour pattern on neck and forebody light reddish, pink ("salmon-coloured"), orange or yellowish, with broad irregular transverse blotches, either olive or dark brown and usually edged with black, or generally darkened. Dorsal markings broadest in vertebral area; usually not including lowermost longitudinal scale rows. Borders of blotches distinctly jagged and lighter interspaces mottled with short olive or black lines, particularly in the midbody region (Plate 1). Apical pits may be distinctly pigmented with black (e.g., NMW 25447.10). Posterior part of body and tail uniformly olive or darkened. Venter reddish, orange (e.g., MHNG 2610.88), yellowish or pale olive; toward midbody and posteriorly lateral edges of ventrals mottled with black flecks or impinged upon by darker dorsal coloration; underside sometimes uniformly dark posteriorly. In some individuals (e.g., BMNH 1965.1460), dorsal pattern only visible on neck and foremost part of trunk, remainder of body and tail uniformly darkened. A juvenile specimen (probably BMNH 1962.937) was "canary yellow, barred dorsally with bright cobalt blue" when alive (Corkill & Cochrane, 1966).

PLATE 1

Male (MHNG 2610.88, above) and female (MHNG 2610.89) specimen of *Hemerophis socotrae*.

The maxilla has 17-20 teeth, the last two usually enlarged and separated by a diastema of variable size (comparatively narrow or distinct), last tooth not or only slightly offset laterad. Counts for remaining dentigerous bones are 9-12 (palatinum), 23-28 (pterygoid), and 20-22 (dental), respectively (vouchers BMNH 1962.936, MHNG 2610.88, NMW 25447.8, and NMW 25467). Palatine processus of maxilla with a long straight lateral border (Fig. 3). Posterior tip of lateral processus of palatinum not reaching distinctly beyond anterior extension of choanal processus. Pterygoid constricted behind lateral processus (Fig. 4). Anterior projection of basisphenoid (i.e., parasphenoid) basally constricted, transverse ridges slightly concave, crista basisphenoidea poorly developed, postero-lateral area (Vidian foramen) with a distinct emargination (Fig. 5).

Hypapophyses developed to the heart region (lacking posteriorly, fide Boulenger, 1893). Articular surface of prezygapophyses of midbody vertebrae semi-orbicular, accessory process distally obtuse, dorsal border of zygosphene convex. Length of midbody vertebra centrum divided by least width of neural arch (lc/wn) 1.32-1.36, length of centrum / width across prezygapophyses between outer edge of articular facets (lc/wp) 0.73-0.77, length of neural crest / least width of neural arch (nc/wn) 1.00-1.06 (MHNG 2581.92). Proportions for vertebrae from the anterior and posterior region 1.23-1.27 (lc/wn), 0.70-0.73 (lc/wp), and 0.94-1.00 (nc/wn), respectively (based on a single vertebra, see Material and methods).

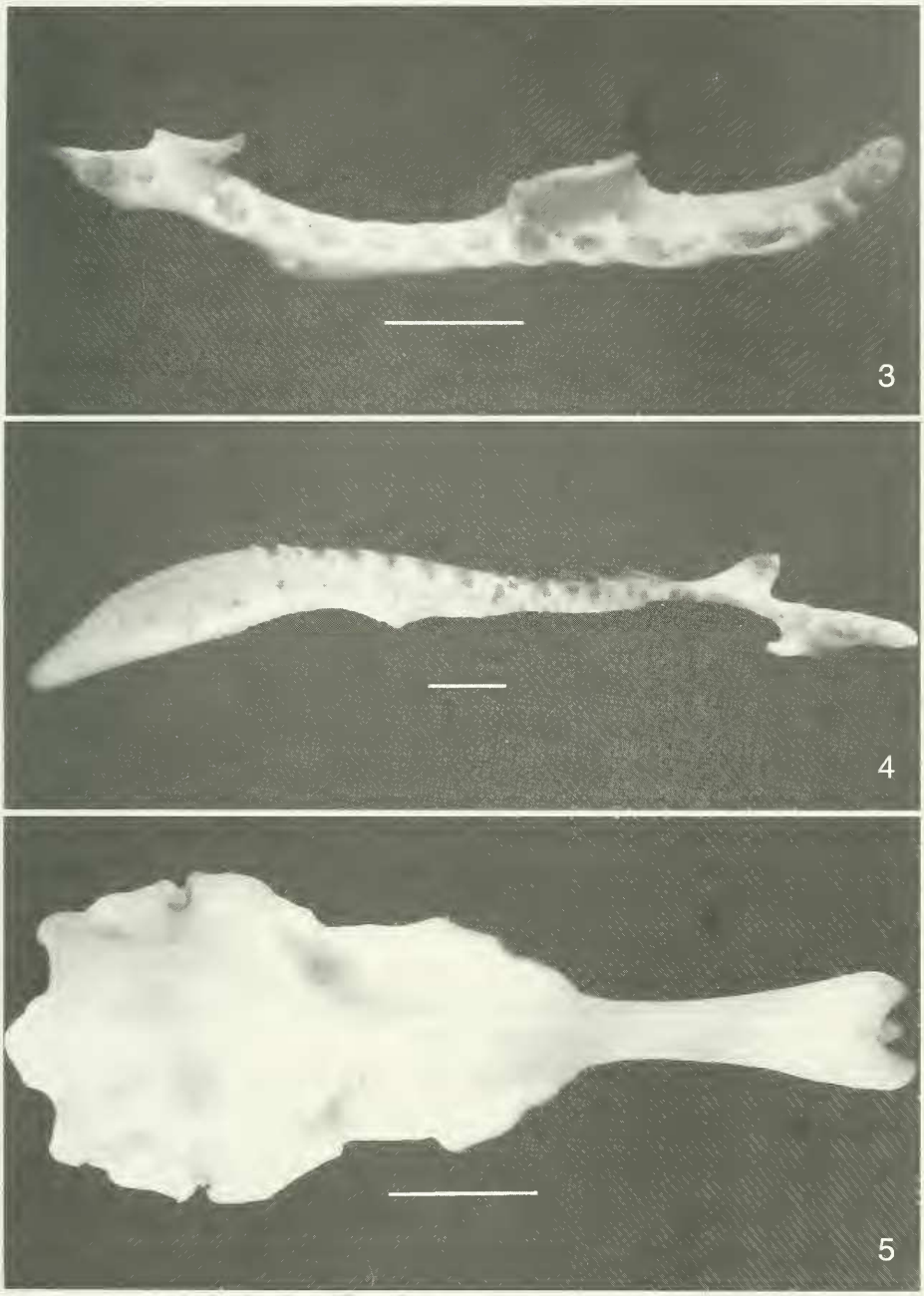
Posterior tip of heart at level of ventral 56 or 57 (25% vs, n=2), liver situated between ventral 67 and 116 (29-52%), anterior tip of pancreas 137-141 (60-62%), right testes 173-180 (75-79%), left testes 181-193 (80-83.5%), and right kidney 192-213 (85-92%) in five males and a female specimen checked for these features (see Material and methods).

Hemipenis subcylindrical, distinctly spinose at the basis, sulcus spermaticus simple (undivided); spines reducing in size toward central part of organ; distally with spinulate (denticulate) retiform ridges on the asulcate side and furrow-like perpendicular depressions along the sulcus spermaticus (Fig. 6a). Apex in situ reaching to subcaudals 8-9 (c. 6.5-7.5% cs). Insertion of *M. retractor penis magnus* at subcaudal 22-24 (18-20%).

Samhah population. In terms of external morphology including colour pattern, the Samhah population (NMW sample) is generally similar to Sokotra specimens except for its slightly larger number of ventral scales, i.e., 231 in one male (NMW 25447.5) and 228-237 in four females (instead of 217-227 and 222-231, respectively, for the Sokotra sample).

Distribution and natural history notes. *Hemerophis socotrae* is recorded from Sokotra and Samhah, an island situated c. 50 km southwest of Ras Shuab, the western tip of Sokotra. Samhah and its sister island Darsa are commonly referred to as The Brothers (al-Ikhwan).

On Sokotra, the species was collected from the Noged Plain along the southern coast (i.e., at Aqarhi ["Hakari"] or from the mouth of Wadi Falanj, Steindachner, 1903) and the northern littoral between Qalansiyah and Ras Momi, notably at "Hasu", around Ghubbah, in the vicinity of Diham (e.g., BMNH 1965.1460), from the plain



FIGS 3 – 5
Left maxilla (3), left palatinum and pterygoid (4), and basisphenoid (5) of *Hemerophis socotrae* (MHNG 2610.88). Lines equal 2 mm.

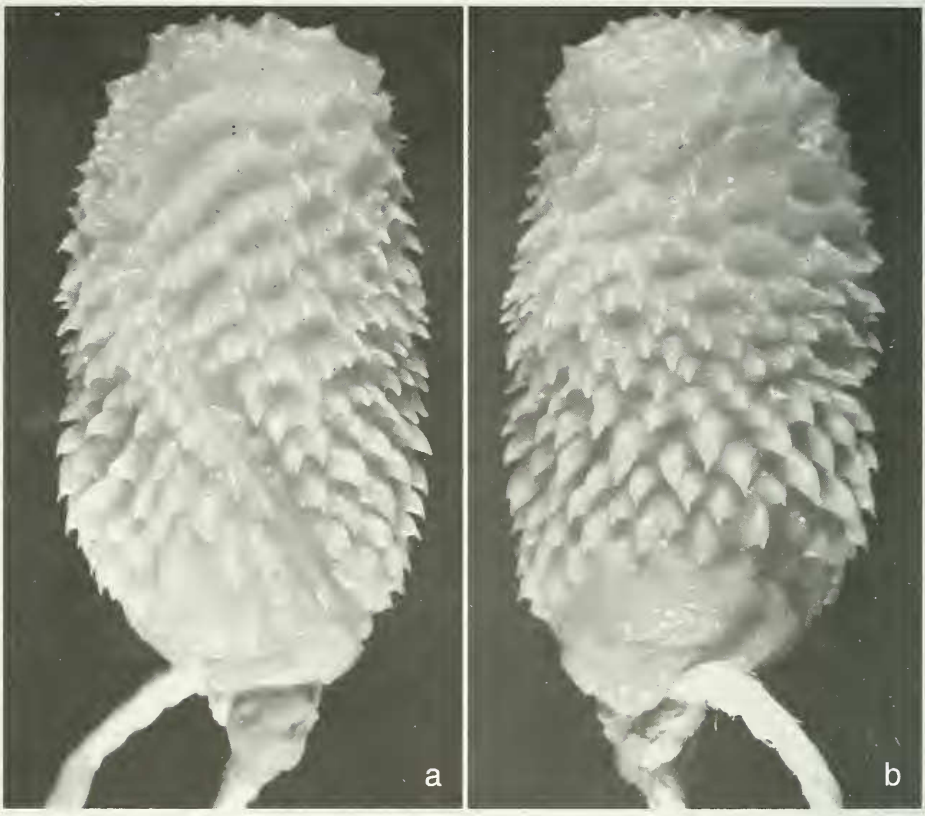


FIG. 6

Sulcate (a) and asulcate view of the everted right hemipenis of *Hemerophis socotrae* (MHNG 2610.88). Original length 15 mm. Photo B. Cerotti.

and hills near Hadibu including Hawlaf and Wadi Manifoh, and at Fikhah near the eastern tip (Ras Momi) of the island (Bent & Bent, 1900; Boulenger, 1903; Corkill & Cochrane, 1966; Showler, 1994; Wranik, 1998).

Some specimens from Sokotra including the syntypes (Günther, 1881) are without precise locality data. Three individuals obtained by Riebeck & Schweinfurth (Taschenberg, 1883) including MHNG 2443.4 and ZMH 2507 from "Tamarida" may have been collected on the southern slopes of the Hajhir massif or around Hadibu (Schätti & Desvoignes, 1999: footnote 19; the specimen registered in the Berlin collection (ZMB 10114) is missing).

Generally, *Hemerophis socotrae* inhabits rocky areas, hard (compacted) substrata, or fine sandy grounds (Fig. 7). The species is encountered near the course of rivers and creeks, around springs, pools, estuaries or lagoons and elsewhere along the shoreline. NMW 25467, for instance, was collected next to papyrus swamps ("nächst den *Cyperus* Sümpfen") near Qalansiyah (Steindachner, 1903). Bent & Bent

FIG. 7
Habitat of *Hemerophis socotrae* at Fikhah near Ras Momi.

(1900: 376) observed a probably subadult specimen at the mouth of a cave near Ras Momi. All records with definite origins are from lowland stations. However, specimens most probably of this species were sighted among rocks in densely vegetated places below the Dihaal pass at c. 900 m in upper Wadi Qishn (Schätti & Desvoignes, 1999).

Hemerophis socotrae is a most timid, agile, and fast-moving snake hiding at the slightest disturbance. It may, therefore, easily escape the attention of an inexperienced naturalist. This could explain why Ogilvie-Grant & Forbes collected a single female near Hawlaf (BMNH 99.12.5.119) but had not seen any other specimen during their visit of two and a half months in winter 1898/99 (Boulenger, 1903), whereas, virtually simultaneously, the Austrian expedition (O. Simony) obtained at least seven individuals from coastal areas.

Moreover, Simony and his companions collected five specimens on Samhah. This island is devoid of sweet water. There, the snakes were collected among rocks near the coastline ("in Felslöchern nahe dem Strande") where they preyed on small sea fish ("Gobiiden", Simony, 1899).

Hemerophis socotrae is probably most active in the early morning and late afternoon. To judge from observations in the field (i.e., fresh tracks in sand) and in captivity, this species also hunts mice and lizards at night. Neither when captured nor later did any of the collected specimens ever attempt to bite, hence its generic name (see Derivatio nominis).

MHNG 2610.89 laid unfertilised eggs in the last third of September.

Comparative morphology

Hemerophis socotrae differs from Eurasiatic *Hierophis* species in, for instance, a larger number of supralabials (nine or more versus eight in *Hierophis*) of which a single one contacts the eye (two), paired preoculars (single), the reduction pattern of dorsal scale rows on the posterior part of the trunk involving paravertebral rows (instead of purely lateral reductions, except in *H. cypriensis*), and in the position of the testes and kidneys (Schätti, 1987, 1988a; Twerenbold, 1987).

Vis-à-vis *Hierophis* and Saharo-Sindian *Platyceps* species, differences exist in the presence of a posterior subocular (absent in *Hierophis* and most *Platyceps* spp.) and subtemporal scale (absent in both Palaearctic genera), heterogeneous scalation of the second row of dorsals (homogeneous), midbody scale counts (23 rows in *Hemerophis* against 17 or 19), skull bones (e.g., palatinum, basisphenoid), vertebra ratios (particularly lc/wn), and in hemipenis morphology, i.e., shape and ornamentation as well as length of the organ and the *M. retractor penis magnus* (Schätti, 1987, 1988a).

Details of the palatine (e.g., shape of choanal processus) and basisphenoid (area lateralis, transverse ridges), proportions of midbody vertebrae (lc/wp), the position of the gonads and kidneys, and hemipenial ornamentation also separate *Hemerophis socotrae* from *Hemorrhois hippocrepis* and related species (Schätti, 1986b, 1987, 1988b: Fig. 4, 1993b; Twerenbold, 1987).

Zamenis elegantissimus Günther and other Arabian endemics, viz. *Coluber thomasi* Parker (see Incertae sedis) and *Z. variabilis* Boulenger, differ from *Hemerophis socotrae* in various features including fewer supralabials, the absence of a posterior subocular and subtemporal scale, fewer midbody dorsal scale rows (19 or less in Arabian species), a smaller number of teeth on the maxilla (11-15 vs. 17-20), pterygoid (14-19 vs. 23-28) and dental (13-16 vs. 20-22), and in the shape of midbody vertebrae.

Compared with *Coluber florulentus* Geoffroy and related species (see Material and methods), *Hemerophis socotrae* exhibits differences in, for instance, the presence of a posterior subocular (i.e., one supralabial entering the eye), a larger number of teeth on the maxilla (17-20 vs. 14-16 in East African populations of *florulentus* [see below and Appendix], and also 13-16 in *brevis smithi*) and pterygoid (23-28 vs. 18-20 in *florulentus*, Schätti, 1987, 1988b), and in characters separating *Hemerophis* from all Old World racer genera, i.e., the occurrence of a subtemporal and heterogeneous scalation in the second longitudinal row of dorsals.

To conclude from morphological evidence, and without taking into account osteology (e.g., palatinum, basisphenoid, number of teeth on maxilla and pterygoid, vertebrae), visceral topography (testes, kidneys), and hemipenis features, *Hemerophis socotrae* shows a number of derived external features which justify generic status for this taxon. These character states include (mostly) paired preoculars, an increased number of supralabials (nine or more), the presence of a posterior subocular (i.e., a single supralabial entering the eye) and subtemporal, reduction of the posterior chin shields, heterogeneous scalation of second dorsal row, and comparatively high midbody scale counts (23 rows) with paravertebral reductions on the posterior part of the trunk.

For the time being, we are not in a position to designate the sister group of *Hemerophis*. Additional studies, in particular comparison with endemic racer species from the Horn of Africa and further Afrotropical genera, are necessary to clarify the phylogenetic affinities of *H. socotrae* (see Discussion).

PALAEARCTIC AND AFROTROPICAL RACER GENERA

Lumping together 23 Palaearctic and Afrotropical taxa, some of them of doubtful status, Welch (1983) resurrected *Eremiophis* Fitzinger, 1843. This is a nomen dubium (Schätti, 1988a).

Based on morphological characters, Schätti (1986a, 1987, 1988a, etc.) presumed that Palaearctic racers (including Saharo-Sindian species) belong to at least three distinct genera, namely *Hemorrhois* Boie, 1826 (type species *Coluber hippocrepis* Linnaeus), *Hierophis* Fitzinger, 1843 (*C. viridiflavus* Lacépède) and *Platyceps* Blyth, 1860 (*P. subfasciatus* Blyth, syn. *C. ventromaculatus* Gray).

Regarding external morphology, the genus *Hemorrhois* and Saharo-Sindian species of *Platyceps* differ from *Hierophis* spp. in a larger number of supralabials (nine or more versus eight) and the presence of paravertebral reductions of dorsal scale rows (absent in *Hierophis*). Concerning hemipenis features, *Hemorrhois* and *Platyceps* spp. have an organ evenly widened from the base to the apex with irregular apical depressions, instead of distinctly bulbous distally and regularly reticulated as in *Hierophis*. Differences also exist in, for instance, a number of osteological characters (dentigerous bones, neurocranium, and vertebrae) and dorsal colour pattern.

Without taking into account osteological and visceral features for which transformation series and their polarity are not established, *Hierophis* appears to be primitive vis-à-vis *Hemorrhois* and *Platyceps* on the basis of plesiomorphic character states of external morphology such as, for instance, two supralabials entering eye, low number of supralabials, and absence of paravertebral reductions. Striking differences in hemipenis features (see Schätti, 1987: Fig. 3c-e) separate *Hierophis* spp. from the genera *Hemorrhois* and *Platyceps*.

Morphologically, *Tyria najadum* Eichwald and related taxa from the eastern Mediterranean region and the southern Zagros Mountains (Iran) are remarkable for having single instead of paired apical pits. Due to their overall similarity, these whip snake species are assumed to be phylogenetically closest to *Platyceps* spp. (Schätti, 1993a; Schätti & McCarthy, 2001; Schätti *et al.*, 2001).

This is also the case with *Coluber florulentus* Geoffroy and related East African species (see Material and methods). As a matter of fact, there is not a single phylogenetically significant scalation, hemipenis or vertebra feature that seems to distinguish this mainly Afrotropical group from Saharo-Sindian *Platyceps* spp., i.e., *P. karelini* (Brandt), *P. rogersi* (Anderson), *P. rhodorachis* (Jan), and *P. ventromaculatus* (Gray), the type species of this genus (Schätti, 1987: Table 1, Fig. 3f; Schätti, 1988a: Figs 7A and 7D; Schätti, 1988b: Fig. 4). The same applies to the Arabian *Zamenis elegantissimus* Günther that has, for instance, high vertebra ratios typical for most *Platyceps* species (Schätti, 1987: Table 1).

Nucleotide sequences confirm the reality of the genera *Hemorrhois* Boie and *Platyceps* Blyth as well as their monophyletic origin as implied by Schätti (1986b, 1988b, etc.). This radiation group includes *Spalerosophis* Jan (Figs 8-9, see Discussion), a genus comprising Saharo-Sindian and Somalian species.

Hierophis spp. belong to a different cluster of Palaearctic racers. The southern European *H. gemonensis* and *H. viridiflavus* are combined with their eastern Mediterranean presumed congenerics *H. caspius* (this species is also found in the Balkans), *H. jugularis*, and *H. schmidti* by comparatively low bootstrap values (Figs 8-9). Surprisingly, the latter species group includes *Eirenis modestus* (see Discussion).

Molecular data support earlier findings based on morphological evidence, i.e., the assumption that *Coluber nummifer* Reuss and *C. ravergieri* Ménétries from the eastern Mediterranean region to Central Asia are closely related to *Hemorrhois hippocrepis* and *H. algirus* from northern Africa and the Iberian peninsula (Schätti, 1986b, 1987). Sister species status of *nummifer* and *ravergieri* is also supported by electrophoretic data (Helfenberger, unpubl.). These eastern taxa (see below) are herewith formally referred to *Hemorrhois* Boie.

Furthermore, nucleotide sequences confirm a close phylogenetic relationship of the *najadum* and *florulentus* group with Saharo-Sindian racers. Therefore, *Coluber florulentus* Geoffroy, *C.* (s. l.) *largeni* Schätti, *C. taylori* Parker, *Zamenis brevis* Boulenger, the whip snakes *C.* (s. l.) *schmidtleri* Schätti & McCarthy, *Tyria najadum* Eichwald, and *Z. dahlii* var. *collaris* Müller as well as the western Arabian *Z. elegantissimus* Günther are herewith assigned to *Platyceps* Blyth. This genus also includes *Z. variabilis* Boulenger, a southern Arabian endemic species (in prep.).

Some sequenced species exhibit considerable intraspecific molecular distances (Fig. 8) and thus warrant further investigation (see Appendix). In *Platyceps florulentus* and *Spalerosophis diadema*, for instance, pairwise sequence divergence is high (approx. 7%), approaching values found between closely related species (e.g., *P. rhodorachis* and *P. rogersi*). Furthermore, our DNA data argue for a comparatively recent speciation of *Hemorrhois nummifer* from *H. ravergieri*, the latter being paraphyletic.

Incertae sedis

For the time being, nine Old World racer species await definite generic classification. We consider it appropriate and best to retain them in, or refer to, *Coluber* sensu lato. This compilation does not take account of three nominal species: *C. bholanathi* Sharma is probably a junior synonym of *C.* (s. l.) *gracilis*; *C. atayevi* Tunijev & Shammakov and *C. thomasi* Parker may be conspecific with *Platyceps najadum* (Eichwald) and *P. variabilis* (Boulenger), respectively.

Coluber sensu lato is a hotchpotch comprising highly diverse Palaearctic and African taxa, including a few enigmatic species such as *C.* (s. l.) *andreanus* (Werner) from the Zagros Mountains in Iran, *C.* (s. l.) *dorri* (Lataste) from the arid region of West Africa and the Somalian *C.* (s. l.) *scorteccii* (Lanza).

Coluber (s. l.) *andreanus* has single apical pits, merely seven supralabials, enlarged parietals, and thus only a single anterior temporal, extremely high ventral counts in females (not so in males), and a single lateral reduction of dorsal scale rows

which is sometimes lacking (Schätti, 2001a). As to its phylogenetic relationship, Andreas' racer badly requires comparison with *Platyceps najadum*, other Palaearctic racer genera, and *Eirenis* spp.

In terms of external morphology, *Coluber* (s. l.) *dorri* is outstanding among Old World racers for various morphological features including the absence of an anterior subocular, high midbody dorsal scale counts (29-33; 17-19 prior to the anal), and reductions thereof which are confined to lateral levels, i.e., the first involving rows 7-9, the fourth rows 3-6, and the last rows 3-5. The hemipenis is comparatively short and spinose. This western Sahel endemic might only be distantly related to other African racers and is in need of further studies.

Coluber (s. l.) *scorteccii* merits comparison with *Hemerophis socotrae*, Palaearctic and East African racers and supposedly related genera (see Discussion). In any case, *scorteccii* may only be distantly related to other endemics from the Horn of Africa, viz. *C.* (s. l.) *messanai* Schätti & Lanza and *C.* (s. l.) *somalicus* (Boulenger) which are known only from their holotypes. The latter two species most probably belong to the genus *Platyceps* (in prep.).

Coluber (s. l.) *gracilis* (Günther) from northwest India, *C.* (s. l.) *sinai* (Schmidt & Marx), and the Farasan racer *C.* (s. l.) *insulanus* (Mertens) from the southern Red Sea are probably related to *Platyceps* spp. The insular species is only known from the holotype and a sloughed skin (Mertens, 1965).

At the moment, the phylogenetic affinities of *Coluber* (s. l.) *zebrinus* Broadley & Schätti from Namibia are difficult to evaluate because of plesiomorphic conditions in external characters. Additional investigation is required to assess its relationships.

DISCUSSION

Following Parker (1949), Schätti & Desvoignes (1999) considered *Hemerophis socotrae* to be related to East African racers of the *Platyceps florulentus* group. This assumption was based on biogeographical considerations, dorsal scale reduction pattern, i.e., a single lateral fusion and two or more paravertebral reductions, skull bones, and vertebrae. For instance, *H. socotrae* has vertebra ratios mostly within the range of *P. florulentus* (Schätti, 1987: Table 1). The basisphenoid of *P. brevis smithi* (voucher BMNH 1963.51) and that of *H. socotrae* are similar regarding the shape and extent of the area lateralis, the course of the transverse ridges, and the emargination of the postero-lateral area. Moreover, these species show similarities in some aspects of hemipenis morphology, e.g., comparatively short organs with distinct spines restricted to the basal portion (Schätti, 1988b: Fig. 6D).

A considerable number of apomorphic conditions in external morphology, osteological features, details of visceral topography (in particular a caudal shift of the testes and kidneys), hemipenis morphology (apical depressions with spinulate ridges), a transversally blotched dorsal colour pattern, and aspects of behaviour (e.g., no attempt to bite) indicate that *Hemerophis socotrae* occupies an isolated position vis-à-vis Palaearctic and Afrotropical racers.

Based on nucleotide sequences, *Hemerophis* branched off from a hypothetical ancestral stock prior to the radiation leading to recent Old World racer genera (Figs 8-

9). A long independent evolutionary history of *Hemerophis* is in accordance with the isolation of the Sokotra archipelago from the African continent since ancient times.

The present structure and morphology of Sokotra Island is dated "Post-Lower Miocene" (Beydoun & Bichan, 1970). However, the archipelago may have broken away from the Horn of Africa in the Oligocene (25 mybp or older) as a result of the formation of the Gulf of Aden (Girdler, 1984). Some authors postulate that the separation of Sokotra dates back to an even more ancient era (see Schätti & Desvoignes, 1999).

To judge from geological evidence and the relationships of the endemic Sokotran reptile genera, viz. *Haemodracon* Bauer *et al.*, *Hakaria* Steindachner, *Pachycalamus* Günther, and the opisthoglyph *Ditypophis* Günther, there is reason to believe that *H. socotrae* is phylogenetically closest to Afrotropical, and possibly Malagasy, colubrids (see Schätti & Desvoignes, 1999)[1].

Interestingly, with respect to external morphology, *Hemerophis socotrae* is similar to *Coluber* (s. l.) *scorteccii* from the Horn of Africa which is geographically closest to the Sokotra archipelago. The latter species has, for instance, an increased number of supralabials (9-10), a posterior subocular (usually with a series of scales separating the eye from the supralabials) and reduced posterior chin shields (Lanza, 1963: Fig. 1). Scortecci's racer has 27-29 dorsal scale rows at midbody and a reduction pattern involving mostly paravertebral rows, namely four out of five fusions. Derived external character states found in *H. socotrae* and *C.* (s. l.) *scorteccii* are due to parallelism or convergence. In this context, it must be emphasized that a large number of supralabials and midbody scale rows, the presence of a posterior subocular, and paravertebral reductions are characteristic of *Hemorrhois hippocrepis* and related species.

Nagy *et al.* (2000) analysed cytochrome b sequences of *Hemerophis socotrae* and six Palaearctic racers (*algirus*, *caspius*, *gemonensis* [as *laurenti*], *jugularis*, *ravergieri*, and *viridiflavus*, all taxa as *Coluber* spp.). They deduced a different origin of *H. socotrae* ("Phylogenetisch können [...] verschiedene Ursprünge angenommen werden"), supposed Palaearctic species to be monophyletic, and found that *Hemorrhois ravergieri* and *Hierophis caspius* cannot be distinguished ("anhand des Cytochrom b nicht zu unterscheiden"). However, these species have, for instance, completely different hemipenes and basisphenoids (Schätti, 1987: Figs 1 and 3; Schätti, 1988a: Fig. 6; Schätti & Agasian, 1985: Fig. 1) and they clearly belong to distinct genera.

With regard to *Hierophis*, molecular data reveal a western (*H. gemonensis*, *H. viridiflavus*) and eastern species group as was discovered with cytochrome b

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[1] Schätti & Desvoignes (1999) supposed close phylogenetic relationship of *Ditypophis vivax* Günther with Madagascan "lycodontines". This conclusion is based on the stunning resemblance of hemipenis morphology in MHNG 2596.22 with that in the genus *Madagascarophis* Mertens. This specimen agrees with *D. vivax* in scale characters but is outstanding for its striking dorsal colour pattern and a more slender habitus than is usually encountered in this species (Schätti & Desvoignes, 1999: Fig. 40). Therefore, comparison with additional material is required. Further, this qualifies some comments (e.g., Schätti & Desvoignes, 1999: footnote 60) and opens again the debate of phylogenetic affinities of *Ditypophis* with the Southwest African monotypic genus *Pythonodipsas* Günther (Schätti & McCarthy, 1987).

sequences (Nagy *et al.*, 2000). Furthermore, our results indicate that *H. caspius*, *H. jugularis*, and *H. schmidti* form a monophyletic group with *Eirenis modestus*, the type species of this genus. Despite low bootstrap values, this result is confirmed with the consensus and the total evidence approach (Figs 8-9). Based on morphological evidence and mtDNA (unpubl.), the endemic Cyprus racer, *H. cypriensis* (Schätti, 1985), is most closely related to congeneric European species (in prep.).

As far as hemipenis morphology is concerned, there is no doubt that *Eirenis* spp. are very closely related to *Hierophis* Fitzinger (Schätti, 1988a). In particular, the copulatory organ of *E. modestus* is most similar to those of *H. viridiflavus* and *H. jugularis* (Schätti, 1988a: Figs 6A, 6G, and 7I). However, the sister group relationship of Anatolia-Iranian *Eirenis* with eastern *Hierophis* spp. conflicts with other morphological evidence. Apart from apical pits (single in *Eirenis*, paired in *Hierophis*), dwarf snakes differ from *Hierophis* spp. in, for instance, lacking a subocular scale, having fewer supralabials, only a single anterior temporal, and partially absent reductions of dorsal scales (e.g., *Eirenis modestus*, see Schmidtler & Baran, 1993).

Head and body scale rows character states found in *Eirenis* are very probably plesiomorphic. Thus, it has to be concluded that either eastern and western species of *Hierophis* acquired their scalation conditions independently, or that *Eirenis* spp. lost these characters secondarily. Clarification of the phylogenetic relationships of these genera certainly demands further studies, namely the consideration of more characters and additional species including possibly hitherto undescribed taxa. Furthermore, the presumed monophyly of *Eirenis* Jan, as presently understood including the subgenus *Collaria* Docenko as well as *Pseudocyclophis* Boettger (see Docenko, 1989), requires a detailed investigation (J. F. Schmidtler, in litt.).

The phylogeny of Old World racers, i.e., the reality of the genera *Hemorrhois*, *Hierophis*, and *Platyceps* is beyond any doubt. The same overall pattern including the isolated position of *Hemerophis socotrae* results when using Palaearctic ratsnakes (*Elaphe* spp. sensu Helfenberger, 2001) as outgroup species (in prep.).

Morphological evidence (see above) as well as nucleotide sequences of 12S rDNA and COI (Figs 8-9) clearly indicate a common origin for the genera *Hemorrhois* and *Platyceps* as well as *Spalerosophis diadema*. Based on molecular data, *Hemorrhois* has, unlike *Platyceps*, a clear intrageneric structure.

Irrespective of the method used (maximum likelihood, maximum parsimony, neighbour joining), all phylogenies which are inferred from the combined data set of both DNA fragments result in similar topologies except for the branching pattern within *Platyceps* and the position of *Spalerosophis diadema*.

Using neighbour joining analysis and the GTR+G+I model from the combined data set, *Platyceps elegantissimus* and *P. ventromaculatus* appear as the sister group of all other species in this genus, whereas the Jukes-Cantor model (Fig. 8) assigns this position to *P. florulentus, P. rhodorachis*, and *P. rogersi*. In the case of the maximum likelihood analyses with both models, *P. florulentus* is the sister species of the remaining congeneric taxa. The maximum parsimony analysis places *P. rhodorachis* and *P. rogersi* as a group opposed to the other species of *Platyceps*. The strict consensus approach also produces a topology with an unresolved branching pattern

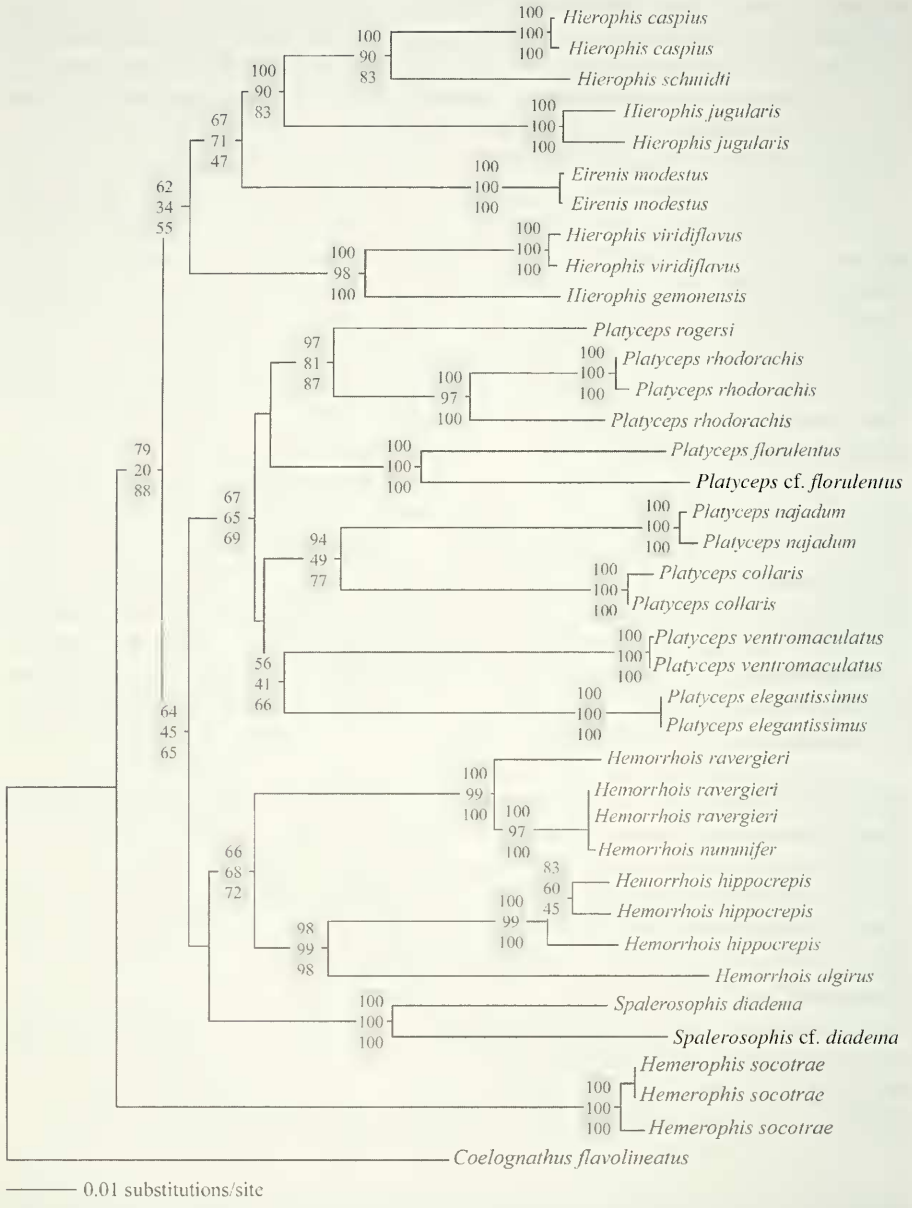

FIG. 8

Neighbour joining tree with the Jukes-Cantor substitution model based on combined data sets of COI and 12S rDNA (1125 base pairs). Numbers above branches represent neighbour joining bootstrap support with 1000 replicates, those on the branches are based on 100 replicates under maximum likelihood and a GTR+G+I model, and those below from 1000 replicates under maximum parsimony including gaps as a fifth state. Bootstrap values are shown for all nodes where support under at least one algorithm is greater than 50%.

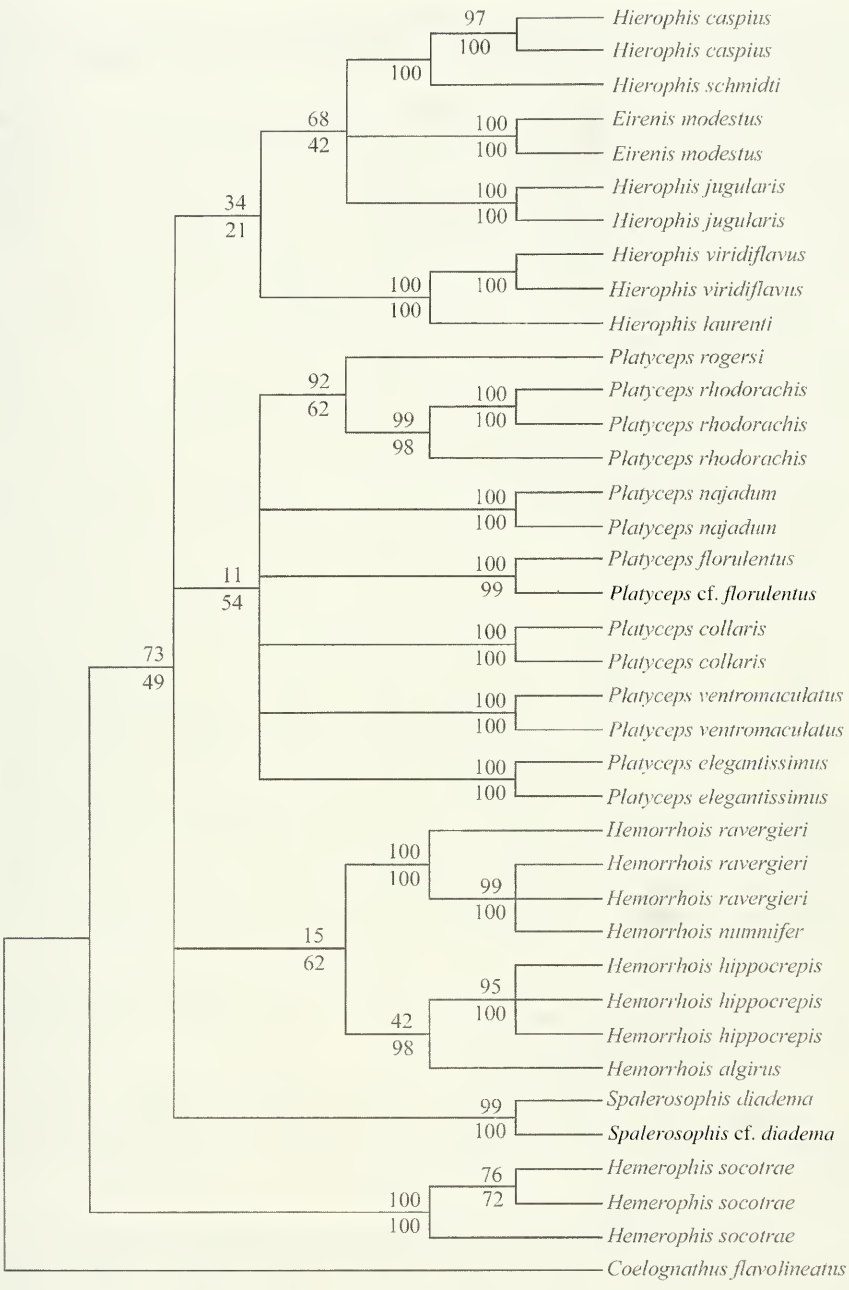

FIG. 9

Strict consensus tree of separately calculated neighbour joining trees of COI and 12S rDNA. Bootstrap values over 50% calculated from 1000 nonparametric replicates are shown. Values above the branches are from the COI data set, using a HKY+G model, and those below from the 12S rDNA data with Jukes-Cantor distances.

within this genus (Fig. 9). Apparently, this discrepancy cannot be resolved with the molecular markers analysed in the present study and must be addressed using alternative genes.

Irrespective of the model of DNA evolution, maximum likelihood analyses place *Spalerosophis diadema* as the sister taxon of *Platyceps*. Neighbour joining and maximum parsimony analyses group *S. diadema* with *Hemorrhois*. This uncertain position is reflected by low bootstrap values (< 50%, Fig. 8). Because of this, we continue, at least for the time being, to consider *Spalerosophis* to be most closely related to *Hemorrhois* spp. (Schätti, 1986a, 1986b; Schätti & McCarthy, 1987).

The result of the ILD test for the two partitions of 12S rDNA and COI is significant at a low level ($P = 0.046$). Subsequent shuffling procedure with eight replicate P values for each of five re-shufflings was performed to calculate a linear regression slope for each data set (Fig. 10). The stable slope of zero ($P = 0.617$) for the shuffled COI partition suggests that the significance of the original ILD test is a consequence of multiple substitutions rather than structured contradictory information. In contrast, the values increased with fast and significant incline ($P = 0.002$) when the less noisy 12S rDNA was shuffled. Presumably, it converges to a value that normally is observed when the differences of phylogenetic information within each data set are as similar as between each data set ($P \approx 50\%$), i.e., when both are perfectly congruent, or completely saturated at random. Consequently, the increase of the P values is a clear indication that relatively few saturation events occurred in the 12S rDNA prior to shuffling. It leads to the visualisation of structured phylogenetic information of the 12S rDNA and confirms the noisy nature of the COI partition.

In contrast to an incongruent data set, noise can provide traces of congruent information. However, the obstructing effects of noise can be minimized with an appropriate model of DNA evolution. These findings suggest that combining and analysing both data sets is justified (Fig. 8). For comparison, the more conservative approach of evaluating the two data sets separately and combining the results in a strict consensus tree (Fig. 9) was also pursued. For this purpose, the neighbour joining tree of the 12S rDNA data set without a noticeable amount of noise was calculated from Jukes-Cantor distances. This measure gives each mutation equal weight and is considered to be appropriate because the 12S rDNA data set did not show any sign of saturation in the preceding analyses (Fig. 1).

The neighbour joining tree of the COI data set containing obvious homoplasies was calculated from a more complex HKY+G model that counts each specific mutation event differently. This is judged to be suitable for the COI partition because it identifies characters with high mutation frequencies and consequently downweights sites affected by homoplasy.

Using Jukes-Cantor distances, a UPGMA tree resulted in a similar topology as the neighbour joining tree (Fig. 8) with only minor differences in the branching pattern within *Platyceps*. In particular, the monophyly of the different genera and comparable branch lengths are retained. Consequently, mutations occurred with similar frequencies in each branch, and the neighbour joining tree comes close to a molecular clock, i.e., reflects the historical events in chronologically correct order.

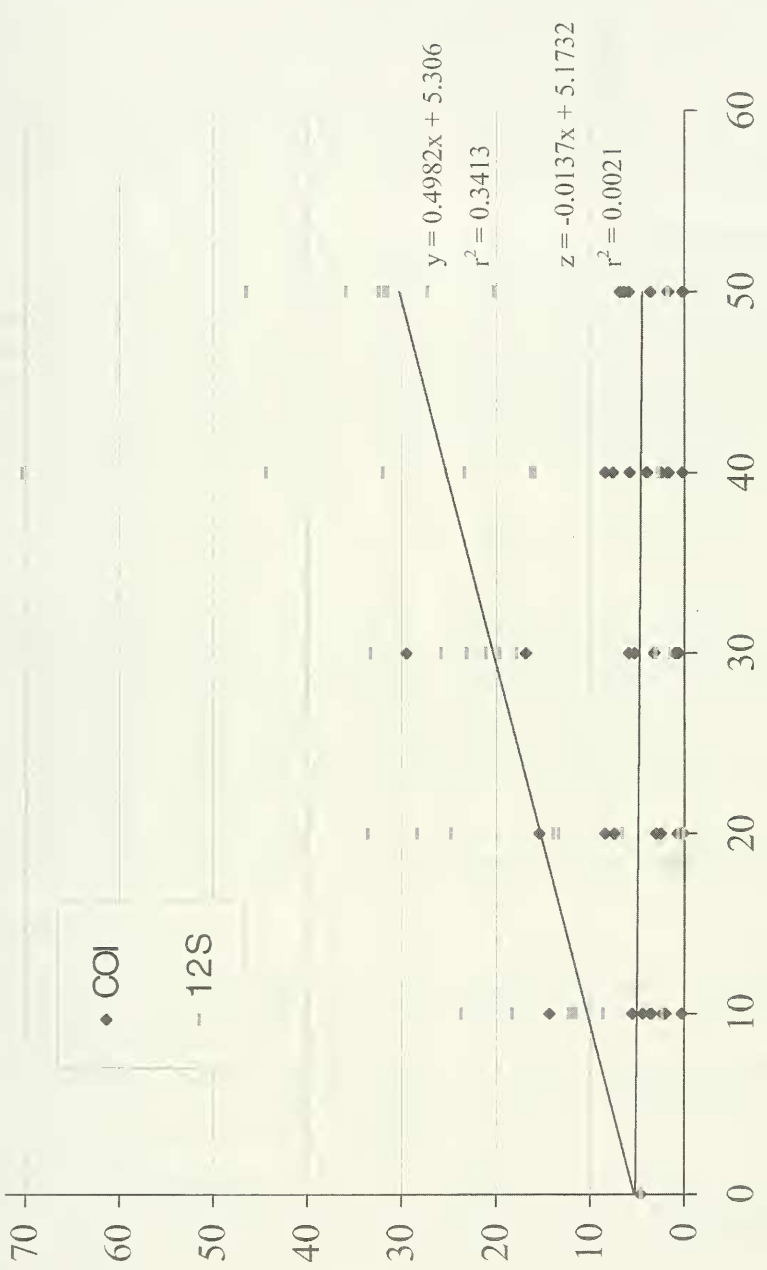

FIG. 10. *P* values of the ILD test after eight runs with a discrete number of shuffled characters in the 12S rDNA and COI sequence.

12S rRNA and COI are often used in phylogenetic analyses, with a generally good performance on different taxonomic levels (e.g., Heise *et al.*, 1995; Zardoya & Meyer, 1996). However, the high proportion of invariable characters and the increasing saturation effects observed, in particular at the third position of the amino acid codon, make the application of COI for systematic purposes in colubrines questionable. Although there is some benefit from this gene in our analyses, the modest results require the testing of additional molecular markers so far little used in phylogenetic analyses.

ACKNOWLEDGEMENTS

We express our most sincere thanks to Vincent Ziswiler for making the molecular investigations possible. E. Nicolas Arnold (London), H.-W. Koepcke (Hamburg), Benedetto Lanza (Firenze), E. Williams (Cambridge), and Franz Tiedemann (Wien) kindly authorised the loans of preserved racers from Sokotra. Colin McCarthy (London) and the Vienna staff checked some scalation features of a few specimens in their care. Notker Helfenberger (Berg) provided tissue samples and protein data. We are grateful to Konrad Dolphin (Ascot, Berkshire), Nick Goldman (Cambridge, GB), and Wolf Blanckenhorn (Zürich) for valuable comments and their support of the molecular analysis. Brenden Holland (Honolulu) critically read excerpts of the manuscript. Patrick Deese (San Miguel de Allende), Volker Mahnert (Genève), and Andrea Stutz (Winterthur) provided most effective help during the preparation and editing of this paper. Andrew G. McArthur (Woods Hole), Gerhard Bächli (Zürich), Michael Buchert (Melbourne), Bernard Cerroti and Corinne Charvet (Genève), George C. Fields, Jr. (San Miguel), Hansjürg Hotz (Zürich), Hubert Krättli (Zürich), Heidi Laubscher (Diessenhofen), Malcolm J. Largen (Liverpool), Jocelyne Leclerc (Zürich), Monica Medina (Woods Hole), Paul Monsch (Winterthur), Clemens Müller-Glauser (St. Gallen), David Orme (Ascot), Claude Ratton (Genève), Markus Ruch, Michael Spörri, and Giancarlo Tomio (Zürich), Josef F. Schmidtler (München), as well as Edoardo Zandri and Abdelkader Bensada (Hadibu) contributed in various ways to the present work.

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APPENDIX. DNA samples used for this study. If not otherwise stated, mtDNA from liver was used; in other cases, genomic DNA from muscle (+), liver (*), or skin (#) was sequenced. SH: tissue collection of Notker Helfenberger; SS and SU: collections of the senior and junior author. *Coelognathus* [*Elaphe*] *flavolineatus* (Schlegel, 1837): *SH 1077 (Java). – *Eirenis modestus* ssp. (Martin, 1838): SH 1115 (Turkey, Konya Prov.), SH 1117 (Turkey, Kars [village]). – *Hemorrhois socotrae*: *MHNG 2610.88 (Sokotra, Wadi Qishn), #MHNG 2610.89-90 (Sokotra, Fikhah). – *Hemorrhois algirus* (Jan, 1863): +MHNG 2415.6 (Tunisia, Tozeur). *H. hippocrepis* (Linnaeus, 1758): #SU 5 (Morocco), +MHNG 2415.94 (Morocco, Agadir area), +MHNG 2415.100 (Morocco, Rabat area). *H. nummifer* (Reuss, 1834): SH 548 (?Turkmenistan). *H. ravergieri* (Ménétries, 1832): SH 561 (Turkey), SH 1287 and 1291 (Kazakhstan). – *Hierophis caspius* (Gmelin, 1789): SH 547 (Ukraine), SH 1148 (Turkey). *H. gemonensis* (Laurenti, 1768): SH 557 (Greece). *H. jugularis* (Linnaeus, 1758): MHNG 2542.96 (Turkey), SH 1080 (Turkey). *H. schmidti* (Nikolskij, 1909): SH 964 (Turkey). *H. viridiflavus* (Lacépède, 1789): +SU 2-3 (Sardinia). – *Platyceps collaris* (Müller, 1878): +MHNG 2447.74-75 (Israel, Tel Aviv). *P. elegantissimus* (Günther, 1879): +MHNG 2456.72 (Saudi Arabia, Taif-Abha), +MHNG 2542.6 (Saudi Arabia, S of Taif). *P. florulentus* (Geoffroy, 1827): +SS 11 (Egypt). *P.* cf. *florulentus*: MHNG 2574.82 (Ethiopia). *P. najadum* (Eichwald, 1831): MHNG 2542.88 (Turkey), +MHNG 2447.53 (Greece, Lamia). *P. rhodorachis* (Jan, 1863): *MHNG 2542.47 (Yemen: Wadi Warazan), *MHNG 2554.13 (Yemen: Jabal Mafluq), *MHNG 2554.14 (Yemen: Wadi Mahsoos). *P. rogersi* (Anderson, 1893): +SS 16 (Israel). *P. variabilis* (Boulenger, 1905): +MHNG 2456.71 (Yemen: Wadi Damad). *P. ventromaculatus* (Gray, 1834): +MHNG 2443.10 (Pakistan), +SS 5 (origin to be verified). – *Spalerosophis* cf. *diadema* (Schlegel, 1837): MHNG 2547.44 (Yemen: Az-Zaydiyah), +MHNG 2414.68 (Pakistan).